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Global warming-induced temperature effects to intertidal tropical and temperate meiobenthic communities

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ABSTRACT

Global climate change and the related temperature rise strongly impact marine life and have long been in the center of scientific attention. This experimental work investigates thermal-stress effects on intertidal meiofauna from tropical and temperate coasts, focusing on community responses. Natural communities were exposed for a month to ambient, elevated constant temperatures and diurnal fluctuating temperature regimes with elevated peak maxima, to mimic realistic future climate conditions. Abundance, biodiversity, community composition and functional diversity were assessed. Differential responses between a tropical and a temperate community were revealed. The tropical nematode assemblage was more tolerant to the elevated constant than to the fluctuating temperature regime, whereas the temperate assemblage was equally affected by both. Shifts in dominance of temperature-tolerant species in elevated constant and fluctuating temperature treatments (due to temperature variations) were observed and explained by a combination of differential tolerances and shifts in species interactions. Overall, global warming-induced temperature was found to alter species dynamics within meiobenthic communities, which may have further implications for the ecosystem.

1. Introduction

Climate change is impacting marine ecosystems on a global scale (Harley et al., 2006; IPCC, 2014). Increasing water temperature and decreasing ocean pH are among the most severe consequences of climate change for marine ecosystems (Brierley and Kingsford, 2009; IPCC, 2014). Global sea surface temperatures (SST) have increased by ca. 0.8 °C over the past 100 years, with 75% of the increase occurring since 1980 (National Research Council, 2011). Climate change models predict a further SST increase of ca. 1 °C up to 4 °C by the end of the 21st Century (Collins et al., 2013; IPCC, 2014). Apart from the increase in mean SST, climate change is predicted to cause a higher frequency of episodic extreme temperature maxima during heat waves, but also to alter amplitudes of diurnal temperature fluctuations, as daily minima and maxima are expected to increase but not necessarily at the same rate (Easterling et al., 2000; Meehl et al., 2000). Such changes can affect the fitness of species (Brakefield and Kesbeke, 1997; Fischer et al., 2011) and/or interspecific interactions (De Meester et al., 2015; Vafeiadou et al., 2018).

Temperature rise being more pronounced in coastal compared to open-ocean waters, shallow coastal marine environments are particularly prone to the effects of climate change (Alsterberg et al., 2011; Harley et al., 2006). Intertidal organisms are subject to both increased SST and elevated air temperatures during some hours every day, especially at the high intertidal zone during low tide. Fluctuating temperatures associated with the tidal regime may support the development of resilience to temperature variability in intertidal organisms (Godbold and Solan, 2013; Sgrò et al., 2011). Yet, temperature extremes and changing fluctuations may have more severe effects on the high intertidal than subtidal organisms, as they may strongly impact the abundance/presence of the most vulnerable species, and consequently lead to local extinctions and reduced structural or functional diversity (Brierley and Kingsford, 2009; Danovaro et al., 2004; Wernberg et al., 2011), provoking changes in ecosystem functioning (Lejeusne et al., 2010).

Meiobenthic communities, of which marine nematodes are the most abundant taxon (Heip et al., 1985), can be strongly affected by changing temperature regimes, with negative effects on density, functional diversity and species evenness (Danovaro et al., 2004). Nematodes and their assemblages usually encompass a high taxonomic and functional

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diversity (Giere, 2009), likely including a range of responses to thermal stress, from vulnerable to tolerant. Therefore, shifts in nematode assemblages can be good bio-indicators of environmental change (Balsamo et al., 2012; Bongers and Ferris, 1999), and thus, of climate change impacts in marine ecosystems.

Most research has focused on individual species responses to global warming (Ingels et al., 2012; Macheriotou et al., 2015; Mayor et al., 2012; Melatunan et al., 2013) or on dedicated species interactions (De Meester et al., 2015; Vafeiadou et al., 2018). But while individual species have different tolerance limits to temperature regime changes, communities may be more resilient (Fields et al., 1993; Gilman et al., 2010). Hence, both population and community-level approaches are necessary to unravel the mechanisms behind climate-change responses (Ingels et al., 2012; Russell et al., 2011). A number of experimental studies have focused on the effects of constant elevated temperatures in combination with pH changes on meiobenthic communities (e.g., Mevenkamp et al., 2018 and Sarmento et al., 2017a for temperate shallow waters; Sarmento et al., 2015, 2017b for tropical coral reefs) and on nematode assemblage responses in particular (Meadows et al., 2015 and Ingels et al., 2018 for temperate shallow waters; Lee et al., 2017 and Gingold et al., 2013 for tropical shallow waters, subtidal and intertidal, respectively, the latter addressing only temperature effects). Nonetheless, to the best of our knowledge, the effects of global warming-induced temperature fluctuations with extreme temperature maxima on meiofauna and nematodes at the community level have hitherto not been investigated.

The present study attempts to reveal the effects of thermal stress, including both an elevated constant and a fluctuating temperature regime with extreme maxima, on meiobenthos communities and nematode assemblages from both a tropical and a temperate intertidal ecosystem. We focus on potential shifts in structural and functional diversity as an indication of community/assemblage response to warming. This response depends to a great extent on the physiological sensitivity of the associated species to temperature change (Somero, 2010). Tropical species are generally more heat-tolerant than temperate ones, due to the natural conditions they live in; however, they can generally be characterized as stenotherms, as they tolerate narrower temperature ranges when compared to temperate species (Deutsch et al., 2008). Stenotherms are expected to be able to cope with only little thermal change, at a pace to which they can acclimatize or adapt, whereas eurytherms are capable of tolerating a wider range of temperatures but at a higher energetic cost (Logan and Buckley, 2015). Tropical intertidal organisms are already living at temperatures close to their upper thermal tolerance limits (Deutsch et al., 2008; Sunday et al., 2014) and often experience habitat temperatures above their physiological optima during heat waves (Nguyen et al., 2011; Somero, 2010). As a result, we anticipate that tolerance to elevated temperature extremes is overall lower for tropical species than for their temperate counterparts. The latter are also expected to be less susceptible to short-term temperature fluctuations due to the greater magnitude of daily temperature range which they typically experience at these higher latitudes.

2. Material and methods

2.1. Sampling sites

Sampling of the tropical meiofauna community was conducted on 22 March 2016 at Praia do Muro Alto, Porto de Galinhas, Pernambuco, Brazil (8°41′13.8″S 34°97′21.7″W), a sheltered sandy beach with scattered mangrove vegetation mainly of *Rhizophora mangle* L., *Laguncularia racemosa* (L.) C.F. Gaertn. and *Avicennia schaueriana* Stapf & Leechm. also being present. Sampling was conducted close to the mangrove area (ca. 100 m distance). Ambient SST and salinity at the time of sampling were 28 °C and 27, respectively. The annual average SST at the site is 27.6 °C, with average annual minima and maxima of 25.7 °C and 29.6 °C, respectively (NOAA; available at www.seatemperature.org; average min. and average max. air temp.: 23 °C and 32 °C, source: NOAA).

Sampling of the temperate meiofauna community was conducted on 25 May 2016 at the Paulina tidal flat in the Scheldt Estuary, The Netherlands (51°20′56.8″N, 3°43′55.4″E). This is an extensive tidal flat with a gradient from muddy to medium sandy sediments and adjacent salt-marsh vegetation, mainly dominated by *Spartina anglica* C.E. Hubb. (Gallucci et al., 2005; Van Colen et al., 2010). Ambient SST at the time of sampling was 16 °C and salinity 25. The annual average SST at the site is 12.6 °C, with average annual minimum and maximum records of 5.1 °C and 20.1 °C, respectively (NOAA; available at www.seatemperature.org; average min. and average max. air temp.: 1.7 °C and 21.3 °C, source: www.scheldemonitor.be/dataportal).

2.2. Collection of samples and acclimatization

Sediment samples were collected at both sites from the high intertidal during low tide. We randomly collected the upper 2 cm of the sediments, and carefully homogenized them on site by gently mixing the sediments with a shovel. Four replicate samples of 5 cm^2 each were haphazardly collected to represent the natural communities or 'field control' and preserved in 4% formaldehyde (in filtered through 32 µm-mesh field seawater) for faunal analysis. An additional 5 cm^2 of sediments were collected for analysis of *TOM* and granulometry. Homogenized sediments were carefully washed through a 2-mm mesh sieve using filtered seawater to remove pebbles, shell debris and large macrofauna, and to break up sediment aggregates. Sieved sediments were subsequently stored in big tanks (40 × 30 × 40 cm), not exceeding a sediment depth of 5 cm to avoid anoxic conditions, with seawater from the field (covering up to 5 cm above sediment surface) and left at ambient water temperature in a controlled-climate room for one week to acclimatize prior to the experiments. Light was controlled in a 12/12 h light/dark cycle using fluorescent lamps connected with timers, and seawater aeration was ensured with continuous O_2 bubbling. Four replicate samples with a surface area of 5 cm^2 each were haphazardly collected from the upper 2 cm of the acclimatized sediments after one week, to represent the acclimatized assemblages or 'T0' prior to the start of the experiment. They were preserved in a solution of 4% formaldehyde in filtered seawater prior to faunal analysis.

Sediment granulometry of the field samples was analysed using a particle-size analyser (Mastersizer 2000, Malvern Instruments) after oven-drying at 60 °C for 48 h. The relative abundances of the different grain size fractions were expressed as % total sample weight. *TOM* was determined from the difference between sediment dry weight after oven-drying at 60 °C for 48 h and the weight after combustion at 450 °C for 8 h, and was expressed as % total dry weight.

2.3. Experimental design

2.3.1. Temperature treatments

Temperature treatments comprised: (a) a constant temperature – control (CT), which corresponded to the ambient water temperature at the time of sampling, (b) an elevated constant temperature (EC), and (c) a fluctuating temperature regime (FT) (Table 1).

The EC temperature in the tropical community experiment (31 °C) was based on the average summer air temperature at the sampling area, considering that air temperatures would be particularly relevant to represent the temperature extremes that high intertidal fauna may experience. The temperature was gradually increased in the microcosms from 28 °C to 31 °C during the first half day of the experiment and thereafter remained constant throughout the duration of the experiment (30 days). The ambient SST at the time of sampling (28 °C) was used for acclimatization and control (CT). The highest temperature used in the FT (36 °C) was chosen as a 5 °C increase of the average summer temperature to resemble an extreme daytime temperature

Table 1
Temperature conditions and abbreviations of the experimental design in the tropical and temperate experiments.

Type of samples	Abbreviations	Time (days)			Temperature (°C)	
		0	15	30	Tropical	Temperate
Field Control	FC				28	16
Acclimatized sediments	T0	T0			28	16
Experimental treatments:						
Constant temp - Control	CT		CT15	CT30	28	16
Elevated constant temp	EC		EC15	EC30	31	21
Fluctuating temp	FT		FT15	FT30	28 - 31 - 36	16 - 21 - 28

during a heat wave (IPCC, 2014; Riahi et al., 2011). The FT was exposed to 28 °C for 3 h per day, then the temperature increased to 31 °C during 3 h and remained stable for another 3 h, then increased to 36 °C during another 3 h and remained stable for another 3 h. Then it decreased back to 28 °C in the reverse order and at a similar pace, resembling a realistic diurnal cycle. This same temperature cycle was repeated daily for the entire experiment duration (30 days; Table 1).

In the temperate community experiment, the EC temperature (21 °C) was based on the average summer air temperature in the area (www.scheldemonitor.be/dataportal). Temperature was gradually increased from 16 °C to 21 °C during the first half day, then remained constant. The ambient SST at the time of sampling (16 °C) was used for acclimatization and control (CT). The highest temperature of the FT (28 °C) was chosen to resemble daily maxima during a heat wave, based on the average summer daytime temperature records in the area (21 °C) (30 °C being the maximum record; www.scheldemonitor.be/dataportal). The temperature increase was thus higher in the temperate than in the tropical experiment, in line with predictions that in Northern Europe, summer daytime high temperatures may increase 2 °C more than the projected increase in mean summer temperatures under RCP 8.5 for 2100 (Collins et al., 2013; IPCC, 2014). In the FT treatment, microcosms were exposed to 16 °C for 3 h, followed by an increase to 21 °C during 3 h, then remained at 21 °C for another 3 h before the temperature increased to 28 °C with the same pace and stabilized for another 3 h. Then it decreased back to minimum with the same pace as described above, in a repetitive cycle for the full duration of the experiment (30 days; Table 1).

2.3.2. Microcosm set-up

The experimental microcosms (Fig. 1) were explicitly designed to prevent oxygen depletion in the sediment pore water. We used 9.5 cm-diameter glass beakers in which a 9 cm-diameter, 1 cm-thick plexiglass disk with a metal sieve (1 mm aperture) on top was deployed at the bottom. 3.5 cm of sediment was added on top of the disk and artificial seawater (ASW) of ambient salinity (27 and 25 for the tropical and temperate experiment, respectively) was added to a height of 5 cm. To prevent sediments and organisms passing through the sieve, it was covered with a 100-µm mesh. Sediments and fauna that passed through this sieve were also collected upon sampling. A 10-cm plastic tube open at both ends was attached to the plexiglass disk. A silicon tube connected to an air pump was attached to this aeration tube creating a negative pressure, as oxygenated water is forced to pass through the sediments from bottom to top and circulate back to the surface. Air pressure was regulated via air pumps of similar capacity, ensuring homogenous sediment oxygenation. We tested that by monitoring the O_2 concentration at 1-mm intervals during a pilot experiment, using a Unisense Oxygen microsensor OX-100 (tip width: 90–110 µm) and Unisense Microprofiling System software.

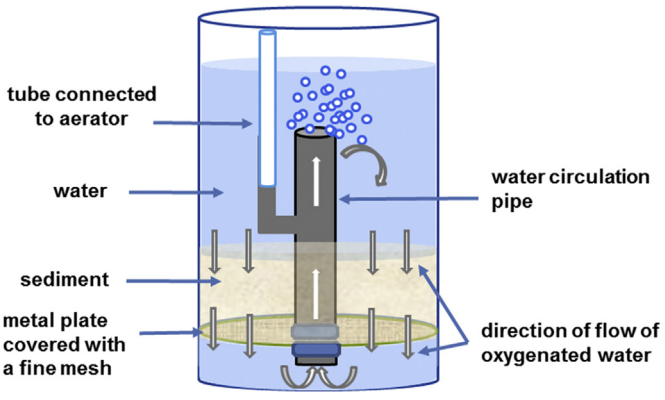

Fig. 1. Design of the microcosm set-up: negative pressure allows oxygenated water to penetrate through the sediments.

Acclimatized sediments (~223 cm^3) were transferred to microcosms, having in total 24 microcosms for each experiment, which were randomly distributed over 6 temperature-controlled (with 100-W thermostats) aquaria (50 × 25 × 30 cm; Fig. 2). Each aquarium corresponded to one of the three temperature treatments for one of two-time destructive sampling events per experiment: Half of the microcosms were sampled after 15 days and half after 30 days of incubation (3 temperature treatments × 2 times × 4 replicates per experiment; Fig. 2). An aeration stone was placed next to each heater to speed up circulation of heated water in the aquaria. The aquaria with the control microcosms were placed in a different climate room with constant temperature regulation in the Marine Biology lab of Ghent University in Belgium, whereas the analogous aquaria for the experimental treatments were placed in another controlled climate room and were temperature-regulated with 100-W thermostats. All aquaria for the tropical experiment were placed in the same climate room with constant temperature regulation, and experimental treatments were temperature-regulated using 100W thermostats, in the LACIMME lab of the Federal University of Pernambuco in Brazil. To prevent evaporation and a concomitant salinity increase, a transparent plastic cover was used. Salinity in the microcosms was checked daily during the experiment and adjusted when necessary using distilled water.

2.4. Faunal analysis

Samples were collected after 15 and 30 days from the respective experimental microcosms. Five cm^2 of sediments down to a depth of 2 cm were collected from each replicate and preserved in 4% formaldehyde. Meiofauna were extracted through centrifugation-flotation using the colloidal silica gel Ludox HS40 at a specific density of 1.18 (Vincx, 1996), counted under a stereomicroscope and identified to their major taxonomic level, i.e., nematodes, copepods, tardigrades, gastrotrichs, etc. In addition, 100 nematode individuals were randomly handpicked and mounted on permanent glass slides using a graded series of ethanol-glycerol solutions (De Grisse, 1969). Nematodes were identified up to the genus or – if possible – the species level using an OLYMPUS BX31 compound microscope, based on the pictorial keys by Platt and Warwick (1988) and the NeMys online database (Guilini et al., 2017).

2.5. Structural and functional diversity of nematode assemblages

We assessed taxonomic diversity based on: abundance (*N*), species richness (*S*), Shannon-Wiener diversity (*H′*), Pielou's evenness (*J′*) and Simpson's diversity (*1-λ′*). The trophic diversity index (*ITD*) and the maturity index (*MI*) were used to assess nematode functional diversity. Trophic diversity was based on the classification by Wieser (1953), which assigns nematodes to one of the following feeding guilds based on buccal cavity characteristics: selective deposit feeders, which are

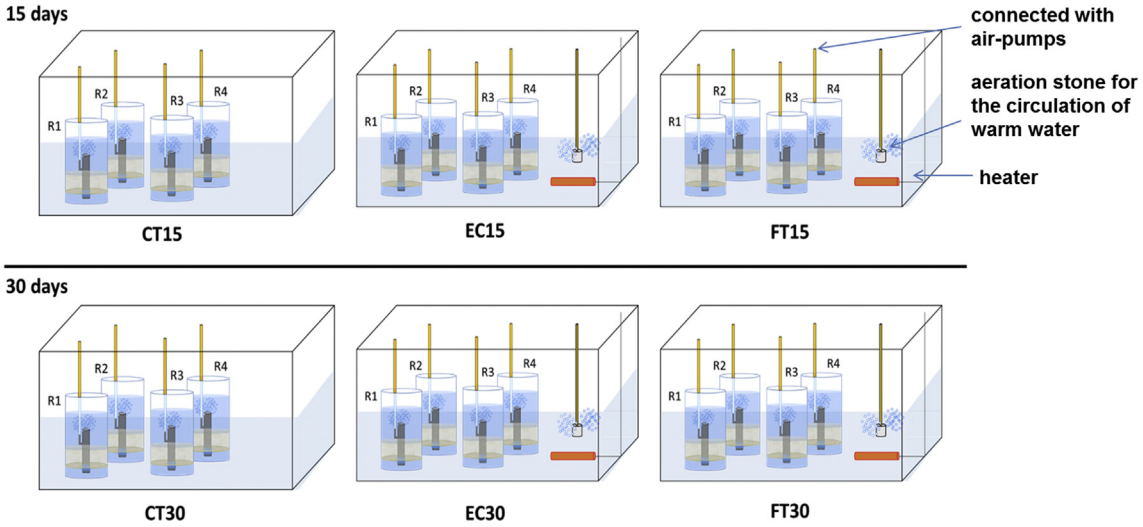

Fig. 2. Experimental design: microcosms were randomly allocated to six aquaria, which correspond to control (CT), elevated constant (EC) and fluctuating temperature (FT) treatments, for 15 and 30 days. Temperature in experimental treatments was controlled with regulated heaters in the aquaria.

essentially bacterivores (1A); non-selective deposit feeders, which ingest mostly unicellular organisms, including various microalgae, bacteria, etc. (1B); epistrate feeders, which are often considered mostly herbivores, feeding on microalgae (2A); and predators/omnivores (2B). *ITD* was calculated as $ITD = \sum_i \theta_i^2$, where θ_i is the relative abundance of the *i*th feeding group (Heip et al., 1985); because *ITD* decreases with increasing trophic diversity, the reciprocal (ITD^{-1}) was used. *MI* was calculated as $MI = \sum_i v(i) \times f(i)$, where *v(i)* is the *c-p* value of the *i*th species and *f(i)* its frequency; a *c-p* value is assigned to each taxon according to its colonization ability, ranging from 1 for extreme colonizers to 5 for very poor colonizers, called persisters (Bongers, 1990).

2.6. Data analysis

Given their different temperature regimes, separate statistical analyses were performed for the tropical and temperate community. Responses to temperature treatments in terms of abundance, diversity and species composition were assessed in order to test the hypotheses that a) the tropical community would be more tolerant to an elevated constant temperature, whereas b) the temperate community would be more tolerant to the daily fluctuating temperature regime with extremes (see further in introduction section). Statistical analyses were performed in R (R Core Team, 2017), except for multivariate analyses which were conducted in PRIMER v6.1.11 with PERMANOVA add-on (Clarke and Gorley, 2006; Anderson et al., 2008).

2.6.1. Experimental enclosure effect testing

Prior to testing the effects of temperature and time on the experimental communities, we tested the 'experimental enclosure' effect for each experiment by comparing abundance, diversity and composition of the control communities between different time moments (i.e., FC, T0, CT15, CT30). We tested this for all the examined variables to avoid misinterpretation of potential temperature effects, using the analogous statistical tests as described below but with Time as a single fixed factor. The Monte Carlo permutation (*p*(*MC*)) was used for PERMANOVA if the number of permutations was < 150 (Anderson et al., 2008).

2.6.2. Univariate temperature responses

Analysis of Variance (ANOVA) was performed on total density data in a two-way crossed factorial design (factors: Temp: 3 levels, fixed; Time: 2 levels, fixed). The assumptions of normality and homoscedasticity were tested using Shapiro-Wilks and Levene's tests, respectively. Total meiofauna and nematode abundances of the tropical assemblage were square-root transformed in order to meet assumptions for parametric tests. Posterior pair-wise comparisons were made with Tukey's Honest Significant Differences (HSD) test.

Univariate two-way Permutational Multivariate Analysis of Variance (PERMANOVA) with the Euclidean Distance similarity measure and 999 permutations (Anderson et al., 2008) was performed in the same crossed factorial design to assess effects of temperature and time on the diversity metrics, as not all data here complied with the assumption of normality. Posterior pair-wise comparisons were performed with PERMANOVA under a reduced model when significant effects were detected (at $\alpha = 0.05$). Permutational Analysis of Multivariate Dispersions (PERMDISP) with 999 permutations (Anderson, 2006) was used to test for homogeneity of multivariate variances between treatments based on mean distances to group centroids for all groups within each factor (i.e., Temp and Time).

2.6.3. Multivariate temperature responses

Assemblage composition was analysed using nematode abundance data after square-root transformation (to scale down the differences between highly abundant and scarcer taxa (Clarke and Gorley, 2006)). Two-way PERMANOVA, using the Bray-Curtis similarity index and 999 unrestricted permutations, was conducted to test the effects of temperature and time on community composition in the same crossed factorial design (see 2.6.1). Pair-wise PERMANOVA was used to further examine significant results (at $\alpha = 0.05$) and PERMDISP to test for the homogeneity of multivariate variances within each factor, as described above. Non-metric multidimensional scaling (nMDS) was used to visualize (dis)similarities in assemblage composition as an effect of temperature and time. Similarly, analysis of the functional group composition in nematode assemblages was performed on the abundance data of the feeding groups. Similarity Percentage Analysis (SIMPER, up to a cumulative (dis)similarity of 90%) was used to determine the relative contribution of species or feeding types to the (dis)similarities within or between groups (i.e., temperature treatments and time).

3. Results

3.1. Tropical community

Sediments of the tropical site were mainly composed of medium sand (250–500 μm), with a median grain size of 469.5 μm and on average 0.7% total organic matter (*TOM*).

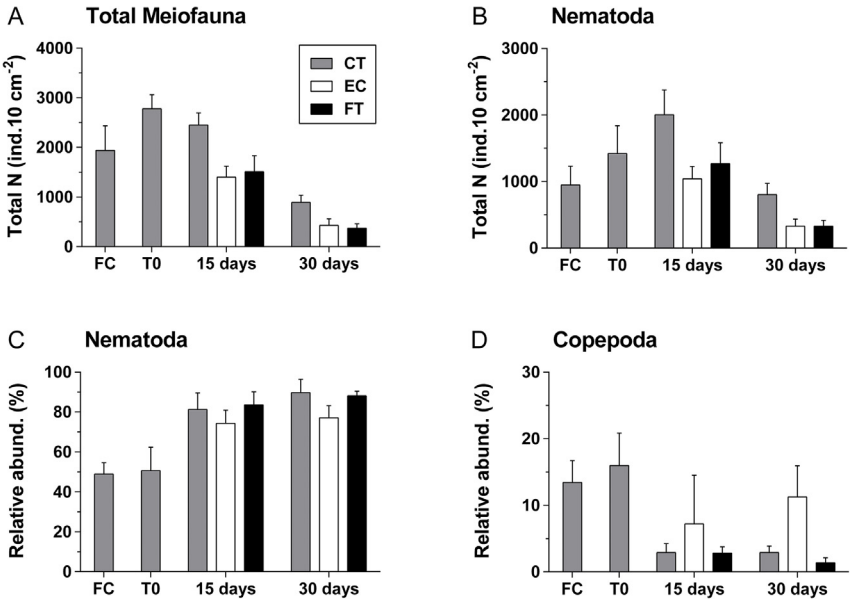

Fig. 3. Absolute (A, B) and relative (%) abundance (C, D) of tropical meiofauna in the field control (FC), acclimatized sediments (T0), control (CT) and experimental treatments: constant elevated temperature (EC) and fluctuating temperature treatment (FT) after 15 and 30 days.

3.1.1. Experimental enclosure effects

Meiofauna densities of the control communities decreased significantly only after 30 days (ANOVA: $F = 14.41$, $p < 0.001$; Tukey HSD for any of the controls vs CT30: $p < 0.001$; FC vs CT30: $p = 0.002$; Fig. 3), which shows that the experimental 'enclosure' effect mostly occurred during the second half of the experiment. Nematode densities followed a similar pattern in time as meiofauna (ANOVA: $F = 11.13$, $p < 0.001$), but were significantly higher in CT15 compared to CT30 or FC (Tukey HSD: $p = 0.001$ and $p = 0.004$, respectively; Fig. 3). A significant effect of time on nematode assemblage structure was evident for the controls (PERMANOVA: $p = 0.001$), PERMDISP results being also significant ($p = 0.006$; Table 2); but CT15 and CT30 clustered together with similar species compositions (pair-wise PERMANOVA: $p(MC) = 0.165$; all other pairs: $p(MC) < 0.05$; Fig. 4A). The feeding group composition of the controls also differed significantly over time ($p = 0.03$), PERMDISP not being significant in this case ($p = 0.09$; Table 2). This significant effect of time reflected the different composition of FC and CT15 ($p(MC) = 0.022$; all other pairs: $p(MC) > 0.05$), mainly due to the higher and lower relative abundances of 2A and 1A nematodes, respectively, in CT15 (Fig. ESM3). None of the diversity indices revealed a significant 'enclosure' effect on the control assemblages (PERMANOVA: $p > 0.05$ for all), apart from S ($p(MC) = 0.009$;

Table 2
Statistical analysis (PERMANOVA and PERMDISP) results for the effects of time on the assemblage structure and diversity metrics of tropical nematofauna of field control, acclimatized sediments and control CT15 and CT30. Significant results ($p < 0.05$) are indicated in bold and with an asterisk.

Control	PERMANOVA						PERMDISP	
Data	Factor	df	MS	Pseudo-F	P(perm)	Unique perms	F	P(perm)
Assemblage Structure	Time	3	1912.10	5.10	**0.001***	997	16.45	**0.006***
	Res	12	374.98					
Feeding Group Composition	Time	3	206.04	22.12	**0.030***	998	4.19	0.093
	Res	12	93.15					
S	Time	3	7.06	6.40	**0.009** [MC]*	43	2.25	0.201
	Res	12	1.10					
J′	Time	3	0.003	1.03	0.438	999	1.79	0.358
	Res	12	0.003					
H′	Time	3	0.07	2.24	0.129	999	0.89	0.711
	Res	12	0.03					
1-λ′	Time	3	0.004	1.45	0.309	998	1.55	0.349
	Res	12	0.002					
ITD^{-1}	Time	3	0.01	0.88	0.512	998	10.90	**0.004***
	Res	12	0.01					
MI	Time	3	0.08	1.29	0.340	927	1.77	0.343
	Res	12	0.06					

[MC] Monte Carlo permutations were used.

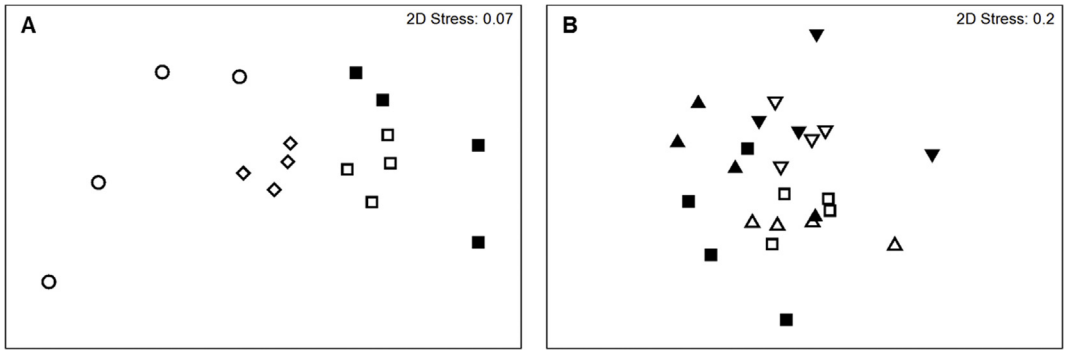

Fig. 4. nMDS ordination based on Bray-Curtis similarity of square-root-transformed tropical and nematode abundance data of the field, acclimatized and control assemblages (A) and of experimental treatments (B). Symbols in (A): ○ field control (FC), ◊ acclimatized sediments (T0), □ control-15 days (CT15) and ■ control 30-days (CT30); in (B): ■ control (CT), ▲ constant elevated temperature (EC) and ▼ fluctuating temperature treatment (FT); hollow symbols: 15 days; solid symbols: 30 days.

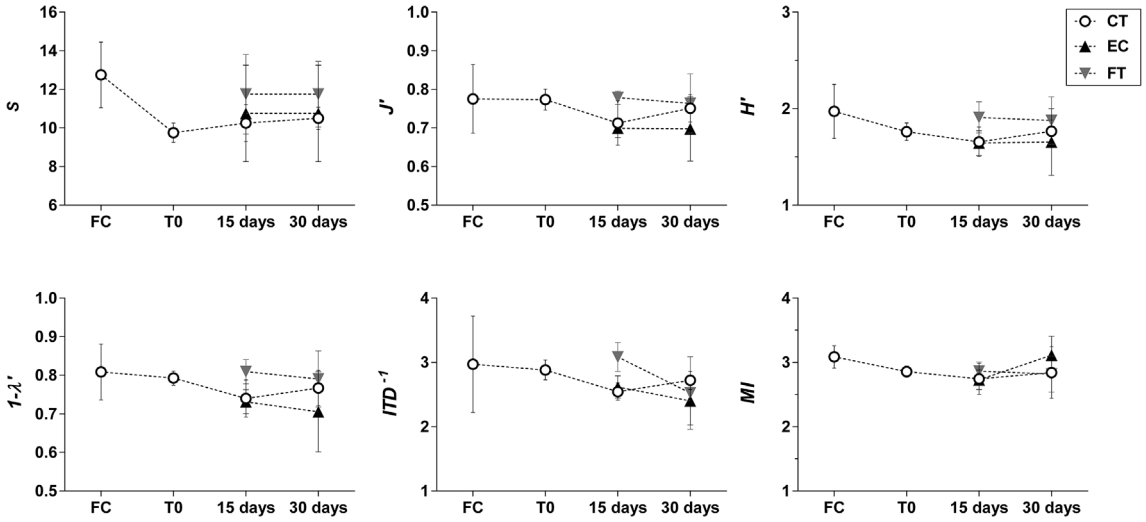

Fig. 5. Structural and functional diversity indices for the tropical nematode assemblages of the field control (FC), acclimatized (T0), control (CT) and experimental treatments: constant elevated temperature (EC) and fluctuating temperature treatment (FT) after 15 and 30 days.

Table 2), which can be attributed to the significantly higher number of species in the FC (pair-wise PERMANOVA: FC vs T0: $p(MC) = 0.008$; FC vs CT15: $p(MC) = 0.043$; FC vs CT30: $p(MC) = 0.045$; Fig. 5). PERMDISP tests for all indices ($p > 0.05$) including S were not significant ($p = 0.201$), apart from ITD^{-1} ($p = 0.004$; Table 2).

3.1.2. Meiofauna densities

Total meiofauna densities of the experimental communities differed significantly as an effect of time (ANOVA: $F = 227.52$, $p < 0.001$) and temperature ($F = 33.07$, $p < 0.001$), independently (temp × time: $F = 0.53$, $p = 0.6$). Meiofauna densities of both temperature treatments were significantly lower than in the control after 15 and 30 days (Tukey HSD for EC or FT vs CT: $p < 0.001$; for EC vs FT: $p = 0.999$; Fig. 3A). Hence, temporal trends were largely independent of temperature treatment, and temperature effects were largely consistent over time.

Nematodes remained the most abundant higher taxon throughout the experiment, followed by copepods (Fig. 3C and D; Fig. ESM1), but their densities decreased significantly with time (ANOVA: $F = 128.8$, $p < 0.001$) and temperature ($F = 25.32$, $p < 0.001$), independently (temp × time: $F = 0.45$, $p = 0.646$; Fig. 3B). No significant difference was found between EC and FT at both moments in time (Tukey HSD: $p = 0.622$), but both treatments yielded lower nematode abundances than the control ($p < 0.001$; Fig. 3B). Like for nematodes, copepod densities were significantly affected by temperature and time (ANOVA: $F = 4.51$, $p = 0.026$; $F = 10.43$, $p = 0.004$) but not in interaction ($F = 0.23$, $p = 0.799$), mainly due to the significantly higher numbers in EC compared to FT at both times (Tukey HSD: $p = 0.021$; Fig. ESM2). Among other meiofauna, tardigrade and ostracod densities were significantly affected by temperature and time, whereas different patterns were observed for the remaining taxa which contributed < 5% to total meiofauna abundances, i.e., polychaetes, oligochaetes, gnathostomulids, turbellarians, gastrotrichs, amphipods, and nauplii (Fig. ESM1; ESM2).

3.1.3. Species composition of tropical nematode assemblages

Thirty-three nematode species (from 31 genera, 17 families) were identified in the tropical assemblages (Table ESM1). Similar to nematode abundances, assemblage structure was significantly affected by temperature ($p = 0.001$) and time ($p = 0.002$), but not in interaction ($p = 0.155$; Table 2). PERMDISP tests were not significant for temperature or the interaction ($p = 0.667$ and $p = 0.459$, respectively), but they were for time ($p = 0.043$; Table 3). Pair-wise comparisons revealed significant differences in assemblage structure between FT and CT ($p = 0.004$) or FT and EC ($p = 0.004$), whereas species composition in CT and EC did not differ significantly ($p = 0.293$; Fig. 4B).

Oncholaimus sp. dominated the FC and T0 assemblages comprising ca. 30% of the total abundance. This species also dominated FT after 15 days (29.8%) and all treatments after 30 days, with the highest relative abundance in EC (Table ESM1). *Paracanthonchus* sp., on the other hand, dominated CT and EC after 15 days (37.8% and 42.3%, respectively;

Table 3
Statistical analysis (PERMANOVA and PERMDISP) results for the effects of temperature and time on the assemblage structure and diversity metrics of tropical nematofauna. Significant results ($p < 0.05$) are indicated in bold and with an asterisk.

Experiment	PERMANOVA						PERMDISP	
Data	Factor	df	MS	Pseudo-F	P(perm)	Unique perms	F	P(perm)
Assemblage Structure	Temp	2	920.09	2.82	**0.001***	999	0.44	0.667
	Time	1	1045.10	3.20	**0.002***	997	5.41	**0.043***
	Temp × Time	2	442.01	1.35	0.155	999	1.57	0.459
	Res	18	326.22					
Feeding Group Composition	Temp	2	125.72	1.41	0.242	999	1.58	0.264
	Time	1	272.54	3.05	**0.048***	998	0.98	0.312
	Temp × Time	2	115.36	1.29	0.281	999	1.19	0.631
	Res	18	89.47					
S	Temp	2	4.04	1.16	0.323	998	2.52	0.116
	Time	1	0.04	0.01	0.913	989	0.31	0.607
	Temp × Time	2	0.04	0.01	0.987	998	0.90	0.656
	Res	18	3.49					
J′	Temp	2	0.01	3.45	0.058	998	0.12	0.912
	Time	1	0.0003	0.10	0.777	998	0.94	0.347
	Temp × Time	2	0.002	0.50	0.605	997	2.21	0.233
	Res	18	0.003					
H′	Temp	2	0.13	2.99	0.060	999	0.83	0.489
	Time	1	0.01	0.12	0.743	997	0.92	0.339
	Temp × Time	2	0.01	0.24	0.775	999	1.87	0.240
	Res	18	0.04					
1-λ′	Temp	2	0.01	3.60	0.051	999	0.53	0.647
	Time	1	0.0002	0.06	0.802	990	2.47	0.127
	Temp × Time	2	0.002	0.44	0.639	999	1.71	0.322
	Res	18	0.004					
ITD^{-1}	Temp	2	0.17	1.81	0.196	998	3.61	0.105
	Time	1	0.24	2.48	0.133	993	1.04	0.311
	Temp × Time	2	0.27	2.80	0.081	998	4.41	**0.045***
	Res	18	0.10					
MI	Temp	2	0.03	0.46	0.622	999	1.21	0.321
	Time	1	0.12	1.75	0.205	997	2.77	0.124
	Temp × Time	2	0.10	1.35	0.278	999	0.78	0.775
	Res	18	0.07					

Table ESM1). SIMPER analysis revealed average similarities in assemblage composition within treatments of 74.1% (EC) to 76.6% (FT), *Paracanthonchus* sp., *Oncholaimus* sp. and *Axonolaimus* sp. always being among the main contributors to these similarities (Table ESM2). Average dissimilarities between treatments ranged from 25.1% between CT and EC to 30% between EC and FT assemblages. Different (combinations of) nematode species were responsible for these dissimilarities; the 6 most contributing species explained > 50% of dissimilarity (Table ESM2). The average dissimilarity between the two sampling times was 27.6%, with *Paracanthonchus* sp., *Oncholaimus* sp. and *Axonolaimus* sp. being the most abundant (in order) species after 15 days, whereas *Paracanthonchus* sp., *Oncholaimus* sp. and *Viscosia* sp.2 were the most abundant after 30 days (Table ESM1; ESM2).

The feeding group composition of FC and T0 was dominated by predatory/omnivorous nematodes (2B: 44.3% and 41.8%, respectively). Non-selective deposit feeders (1B) were the second most abundant group in FC (23.3%), followed by epistrate feeders (2A: 18.3%) and selective deposit feeders (1A: 14.3%). In T0, 2A had a higher relative abundance (32%). By contrast, 1A nematodes were distinctly less abundant in T0 (1%) than in FC; from the three species belonging to the 1A group in FC, only one remained present in T0 (Fig. ESM3; Table ESM1).

The feeding group composition was significantly affected by time (PERMANOVA: $p = 0.048$), but not by temperature ($p = 0.242$) or the temp × time interaction ($p = 0.281$; Table 3). PERMDISP did not reveal any significant results ($p > 0.05$; Table 3). All treatments (control included) resembled the feeding group composition of T0, with only small changes in relative abundances (Fig. ESM3). Differences in time reflected the shift in dominance of the feeding groups 2A and 2B from 15 to 30 days in CT and EC. Hence, all experimental treatments were dominated by 2B nematodes, except for CT15 and EC15, where 2A nematodes dominated. Feeding groups 1A and 1B increased from 15 to 30 days in CT and EC, whereas they both decreased in FT assemblages (Fig. ESM3; Table ESM1).

3.1.4. Structural and functional diversity indices

No significant effect of temperature, time nor their interaction was detected on any of the structural and functional diversity indices in our experiment (PERMANOVA: $p > 0.05$ for all; Table 3; Fig. 5). However, a general trend of higher diversity for FT assemblages was observed (Fig. 5), and the effect of temperature was borderline non-significant for evenness *J′* ($p = 0.058$) and *1-λ′* ($p = 0.051$; Table 3), mainly reflecting a lower diversity in EC than in FT.

3.2. Temperate community

Sediments at the temperate site were characterized by very fine to medium sand (63 μm < 99.75% < 500 μm) with a median grain size of 231.2 μm and on average 1% *TOM*.

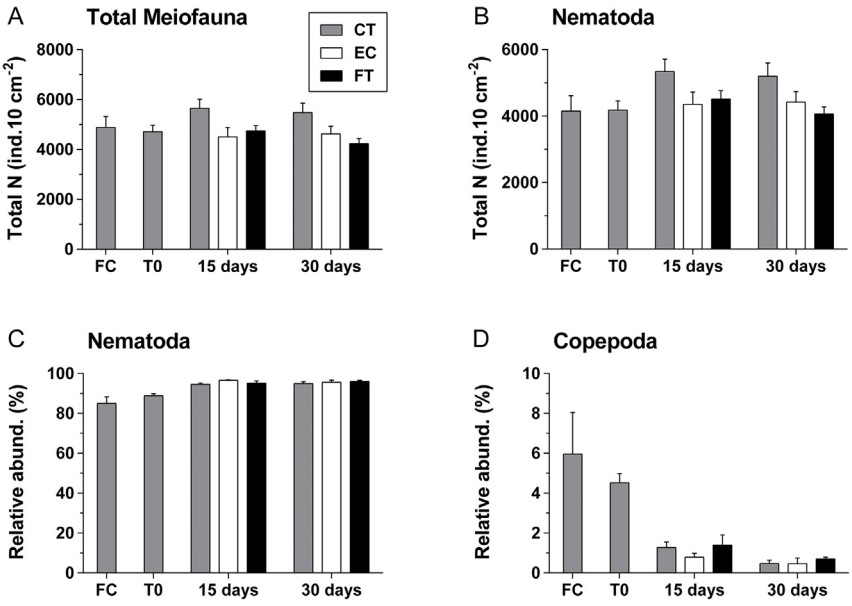

Fig. 6. Absolute (A, B) and relative (%) abundance (C, D) of temperate meiofauna in the field control (FC), acclimatized sediments (T0), control (CT) and experimental treatments: constant elevated temperature (EC) and fluctuating temperature treatment (FT) after 15 and 30 days.

3.2.1. Experimental enclosure effects

Temperate meiofauna maintained their high density throughout the experiment; a significant effect of time (ANOVA: $F = 6.22$, $p = 0.009$) could be attributed to the higher abundances after 15 days (Tukey HSD for CT15 vs FC or T0: $p = 0.049$ and $p = 0.015$, respectively; all other pairs: $p > 0.05$; Fig. 6A). Nematode densities in the control increased significantly after 15 and 30 days compared to both FC and T0 (ANOVA: $F = 11.48$, $p < 0.001$; Tukey HSD: CT15 vs FC or T0: $p = 0.004$ and $p = 0.005$, respectively; CT30 vs FC or T0: $p = 0.009$ and $p = 0.011$, respectively; Fig. 6B). A significant effect of time on nematode assemblage structure was also revealed for the controls (PERMANOVA: $p = 0.001$; Table 4), due to differences between CT15 and T0 or CT30 (pair-wise PERMANOVA: $p(MC) = 0.032$ and $p(MC) = 0.045$, respectively; all other pairs: $p(MC) > 0.05$; Fig. 7A). PERMDISP was not significant ($p = 0.286$; Table 4). Time did not have a significant effect on the feeding group composition of the controls or on any structural and functional diversity metric (PERMANOVA: $p > 0.05$; Table 4). However, the PERMDISP test was significant for *S, H′* and *1-λ′* ($p < 0.05$; Table 4).

3.2.2. Meiofauna densities

Meiofauna of the natural temperate community (FC) reached total

Table 4
Statistical analysis (PERMANOVA and PERMDISP) results for the effects of time on the assemblage structure and diversity metrics of temperate nematofauna of field control, acclimatized sediments and control after 15 (CT15) and 30 (CT30) days of incubation. Significant results ($p < 0.05$) are indicated in bold and with an asterisk.

Control	PERMANOVA						PERMDISP	
Data	Factor	df	MS	Pseudo-F	P(perm)	Unique perms	F	P(perm)
Assemblage Structure	Time	3	558.19	2.13	**0.001***	997	2.38	0.286
	Res	12	262.52					
Feeding Group Composition	Time	3	36.99	1.44	0.244	999	1.60	0.349
	Res	12	25.65					
S	Time	3	9.90	2.11	0.148 [MC]	106	9.79	**0.006***
	Res	12	4.69					
J′	Time	3	0.001	2.60	0.121	998	1.71	0.275
	Res	12	0.001					
H′	Time	3	0.03	1.05	0.407	999	7.19	**0.013***
	Res	12	0.03					
1-λ′	Time	3	< 0.001	0.78	0.531	994	6.24	**0.033***
	Res	12	< 0.001					
ITD^{-1}	Time	3	0.007	0.81	0.515	999	1.28	0.588
	Res	12	0.008					
MI	Time	3	< 0.001	0.34	0.815	502	0.60	0.688
	Res	12	0.01					

[MC] Monte Carlo permutations were used.

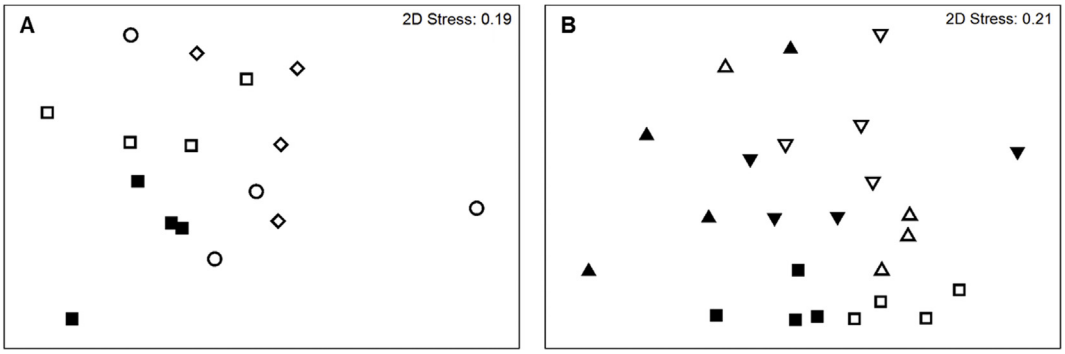

Fig. 7. nMDS ordination based on Bray-Curtis similarity of square-root-transformed temperate nematode abundance data of the field, acclimatized and control assemblages (A) and of experimental treatments (B). Symbols in (A): ○ field control (FC), ◊ acclimatized sediments (T0), □ control-15 days (CT15) and ■ control 30-days (CT30); in (B): ■ control (CT), ▲ constant elevated temperature (EC) and ▼ fluctuating temperature treatment (FT); hollow symbols: 15 days; solid symbols: 30 days.

densities more than twice those of the tropical community (Fig. 6A). Meiofauna maintained their high density throughout the experiment, nematodes being the most abundant taxon, followed by copepods (Fig. 6; Fig. ESM4). Temperature had a significant effect on total meiofauna densities (ANOVA: $F = 29.20$, $p < 0.001$), whereas time ($F = 2.13$, $p = 0.162$) and the temp × time interaction ($F = 2.01$, $p = 0.162$) did not. The temperature effect reflected the lower total meiofauna densities in both temperature treatments compared to the control, at both moments in time (Tukey HSD: EC or FT vs CT: $p < 0.001$ both; EC vs FT: $p = 0.876$; Fig. 6A).

Temperature also significantly negatively affected nematode densities (ANOVA: $F = 22.35$, $p < 0.001$), independent of time (time: $F = 1.68$, $p = 0.211$; temp × time: $F = 1.28$, $p = 0.302$, did not). Nematode densities in both temperature treatments did not differ (Tukey HSD: $p = 0.809$), but both were significantly lower than those of the control at all times ($p < 0.001$ both; Fig. 6B). Copepod densities were significantly lower in the EC compared to the other two treatments but also decreased with time (ANOVA: temp: $F = 6.9$, $p = 0.006$; time: $F = 40.5$, $p < 0.001$; temp × time: $F = 2.25$, $p = 0.134$; Fig. ESM5). Temperature and time both had a significantly negative effect on amphipod and ostracod densities (Fig. ESM5). Other identified major taxa, i.e., polychaetes, oligochaetes, turbellarians, gastrotrichs, gnathostomulids, and nauplii, contributed < 2% to total meiofauna, and apart from oligochaete and turbellarian abundances that reduced at elevated temperatures, no particular patterns were observed (Fig. ESM4; ESM5).

3.2.3. Species composition of temperate nematode assemblages

Thirty-eight nematode species (from 36 genera, 18 families) were identified in the temperate assemblages (Table ESM3). Like nematode abundances, assemblage structure was significantly affected by temperature (PERMANOVA: $p = 0.001$), but in contrast to abundances also by time ($p = 0.004$) and by the temp × time interaction ($p = 0.006$; Table 5). PERMDISP test did not reveal significant results for the interaction ($p = 0.378$) and time ($p = 0.439$), but it was significant for temperature ($p = 0.034$; Table 5). Pair-wise comparisons revealed significant differences between CT15 and FT15 (pair-wise PERMANOVA: $p(MC) = 0.009$), and between CT30 and both EC30 and FT30 ($p(MC) = 0.027$ and $p(MC) = 0.05$, respectively), whereas EC and FT showed similar assemblage structure at both moments in time ($p(MC) = 0.089$ and $p(MC) = 0.061$; Fig. 7B).

SIMPER revealed average similarities in assemblage composition within treatments of 73.5% (EC) to 80.4% (CT). *Bathylaimus* sp. dominated all control assemblages (including FC and T0), and was also one of the most abundant species in other temperature treatments, whereas in EC and FT, *Ascolaimus* sp. was dominant (Table ESM3). *Metachromadora vivipara, Adoncholaimus fuscus* and *Enoploides longispiculosus* were other main contributors to the within-group similarities (Table ESM4). Average dissimilarities between treatments ranged from 26.8% between CT and EC to 29.7% between EC and FT assemblages. Different (combinations of) nematode species were responsible for these dissimilarities (Table ESM4). The average dissimilarity between the two groups in time was 28.4%, with *M. vivipara, Ascolaimus* sp. and *E. longispiculosus* being the most abundant species (in order) after 15 days, whereas *Ascolaimus* sp., *Bathylaimus* sp. and *M. vivipara* were the most abundant after 30 days (Table ESM4).

Non-selective deposit feeders were dominant in FC and T0 (1B: 56.3% and 53.3%, respectively), followed by predators/omnivores (2B: 23.8% and 25.8%), whereas epistrate feeders (2A) and selective deposit feeders (1A) were less abundant (Fig. ESM6; Table ESM3). Significant differences in feeding group composition were observed as a result of temperature, both separately and in interaction with time (PERMANOVA for temp and temp × time: $p = 0.002$ both, time: $p = 0.097$; Table 5). PERMDISP tests did not reveal significant results for any of the factors ($p > 0.05$; Table 5). CT15 and EC15 had a similar feeding group composition (pair-wise PERMANOVA: $p(MC) = 0.226$) and followed the same pattern as FC and T0 (Fig. ESM6). Nevertheless, the most representative species of the dominant feeding group (1B) were not exactly the same in both temperature treatments: *Bathylaimus* sp. was replaced by *Ascolaimus* sp. in EC15, while *E. longispiculosus* remained the most abundant 2B species in CT15 and EC15 (Table ESM3). In CT30, the 2A group became the second most abundant after 1B, and 1A was completely absent. CT30 and FT30 harboured a similar feeding group composition, 1B nematodes remaining dominant (Fig. ESM6). Nevertheless, the most abundant species again shifted; *Ascolaimus* sp. was the first and *Bathylaimus* sp. the second in relative abundance in CT30 and shifted to the opposite in FT30 (Table ESM3). A shift in the proportion of feeding groups was observed also in EC30, 2B nematodes becoming the dominant group (1B being second; Fig. ESM6; Table ESM3).

3.2.4. Structural and functional diversity indices

Structural diversity indices were not significantly affected by temperature, time or their interaction (PERMANOVA: $p > 0.05$ for all; Table 5), despite the generally higher diversity values for CT assemblages (Fig. 8). By contrast, temperature and time in interaction significantly affected the functional diversity metrics (ITD^{-1} and *MI*) (Table 5). ITD^{-1} increased for both CT and EC from 15 to 30 days, whereas the opposite was true for FT (temp and temp × time: $p = 0.009$ and $p = 0.049$, respectively; Table 5). *MI* was also significantly affected by the temperature and time interaction (temp and temp × time: $p = 0.034$ and $p = 0.042$, respectively; Table 5), with significantly higher values in EC30 (Fig. 8). PERMDISP test did not reveal significant results for any factor effects on any index ($p > 0.05$), the only exception being time effects for H' ($p = 0.004$; Table 5).

Table 5
Statistical analysis (PERMANOVA and PERMDISP) results for the effects of temperature and time on the assemblage structure and diversity metrics of temperate nematofauna. Significant results ($p < 0.05$) are indicated in bold and with an asterisk.

Experiment	PERMANOVA						PERMDISP	
Data	Factor	df	MS	Pseudo-F	P(perm)	Unique perms	F	P(perm)
Assemblage Structure	Temp	2	955.84	3.27	**0.001***	999	4.82	**0.034***
	Time	1	1027.90	3.51	**0.004***	999	0.73	0.439
	Temp × Time	2	692.22	2.37	**0.006***	998	1.80	0.378
	Res	18	292.63					
Feeding Group Composition	Temp	2	164.38	7.14	**0.002***	999	1.31	0.304
	Time	1	66.96	2.91	0.097	998	0.23	0.664
	Temp × Time	2	141.13	6.13	**0.002***	998	0.79	0.654
	Res	18	23.03					
S	Temp	2	4.67	1.71	0.217	992	0.78	0.458
	Time	1	< 0.001	0.00	1.000	932	1.48	0.259
	Temp × Time	2	1.50	0.55	0.562	947	1.04	0.554
	Res	18	2.72					
J′	Temp	2	0.003	2.15	0.150	999	0.99	0.460
	Time	1	0.005	3.58	0.078	997	0.31	0.632
	Temp × Time	2	< 0.001	0.25	0.747	999	1.46	0.515
	Res	18	0.001					
H′	Temp	2	0.07	3.17	0.062	999	1.04	0.399
	Time	1	0.04	1.77	0.198	997	10.42	**0.004***
	Temp × Time	2	0.01	0.46	0.635	998	1.24	0.492
	Res	18	0.02					
1-λ′	Temp	2	0.002	2.70	0.097	998	2.64	0.102
	Time	1	< 0.001	0.99	0.338	999	1.49	0.345
	Temp × Time	2	< 0.001	0.21	0.827	999	2.27	0.276
	Res	18	0.001					
ITD^{-1}	Temp	2	0.03	5.95	**0.009***	999	0.18	0.888
	Time	1	0.01	2.56	0.140	995	0.73	0.471
	Temp × Time	2	0.01	3.77	**0.049***	999	1.23	0.610
	Res	18	0.004					
MI	Temp	2	0.05	4.12	**0.034***	998	3.32	0.071
	Time	1	0.10	8.43	**0.012***	996	2.17	0.297
	Temp × Time	2	0.04	3.57	**0.042***	999	1.57	0.569
	Res	18	0.01					

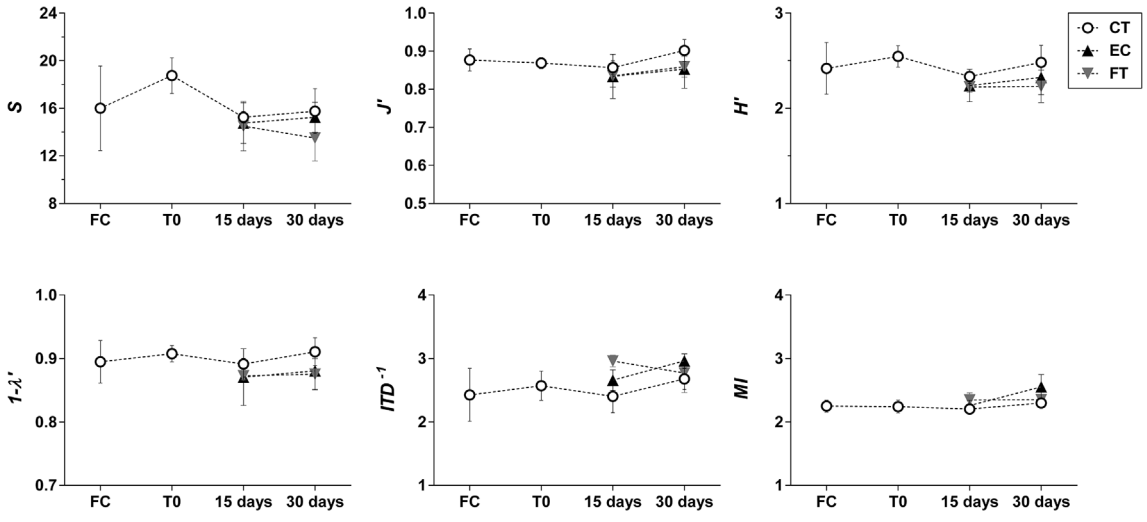

Fig. 8. Structural and functional diversity indices of the temperate nematode assemblages of the field control (FC), acclimatized (T0), control (CT) and experimental treatments: constant elevated temperature (EC) and fluctuating temperature treatment (FT) after 15 and 30 days.

4. Discussion

We examined the response of a tropical and a temperate meiobenthic community, with emphasis on their nematofauna, to constant elevated temperature and fluctuating temperature regimes with elevated maxima. Both temperature regimes used here caused significant changes in both intertidal communities in terms of abundance, community structure and functional diversity. Tropical and temperate communities showed divergent responses to elevated constant and fluctuating temperature in terms of community composition.

4.1. Effects of the experimental enclosure

Time had a negative effect on the absolute abundances of most higher taxa in both the tropical and the temperate community, but nematode abundances responded differentially to time of enclosure between both communities. Nematode abundance decreased to 77.5% of field densities after 30 days in the tropical community but remained high throughout the experiment in the temperate community. The higher meiofauna densities in T0 compared to FC after a week of acclimatization in the tropical community are likely a result of the patchiness in meiofauna distribution and of a redistribution of meiofauna in the sediments during pre-incubation in between field sampling and start of the actual experiment. Note that we collected sediment of the upper 2 cm in the field and stored it in containers in a 5-cm thick layer. It is common that at least nematodes in such thicker sediment layers reposition themselves and concentrate in the uppermost few cm (authors' own unpubl. observ.).

The absence of any decrease in nematode abundance and diversity over a 1-month incubation in the temperate microcosms suggests that our microcosm design (Fig. 1) prohibited hypoxia in contrast to many other microcosm designs for experiments with meiofauna, which generally only aerated the sediment from above. Indeed, substantial decreases in total meiofauna and nematode densities, by up to 75%, are common in micro- and mesocosm experiments (Austen and Warwick, 1995: 60–75% reduction of nematode abundance after 16 weeks in the control of a mesocosm experiment, but no decrease of species richness was found; Gingold et al., 2013: nematode abundance decreased by ~50% after 30 days in the control of a microcosm experiment; Olafsson and Elmgren, 1991: total meiofauna abundance reduced; specifically, nematode abundance declined by 50% and copepod abundance by 90% after 3 weeks in a microcosm experiment; Schratzberger and Warwick, 1999: nematode abundance decreased on average by ~50% (by 48% for sandy and by 56% for muddy sediments) after 8 weeks in a microcosm experiment), and are generally attributed to effects of containment, including lack of normal water and oxygen circulation. Here we maintained oxygenated conditions in the microcosms that resemble natural oxygen conditions in the upper 2 cm of the sediments. Generally sensitive species, such as Chromadoridae, remained present throughout the experimental incubation in both control assemblages, and so did high total nematode abundances in the temperate community. Good oxygen circulation was also achieved in the experimental designs by Sarmento et al. (2015; 2017b), where meiofauna even increased in abundances in the control microcosms.

Predation among meiofauna may be a reason for the divergent response of total nematode densities in the tropical vs the temperate community: In the former, predatory nematodes accounted for ~40% of nematode abundances in controls at the end of the experiment, whereas this was 'only' 24% in the latter. Such high proportions of predacious nematodes can exert a strong top-down control on the abundances of prey taxa (Gallucci et al., 2005; Moens et al., 2000). In addition, turbellarians, polychaetes and tardigrades can also be predators of meiofauna (Giere, 2009) and were more abundant in the tropical than in the temperate communities. Turbellarians, in particular, are often predacious and are more abundant in coarser sediments (Giere, 2009; Martens and Schockaert, 1986); the median grain size in our tropical microcosms was ca. double that of the temperate microcosms. The relative abundance of turbellarians in the tropical community increased in high temperature treatments and towards the end of the experiment, opposing the trend of nematode and total meiobenthos densities. In addition, polychaetes and tardigrades reached up to ~10% of total meiofauna in the tropical, and < 1% in the temperate communities.

4.2. Effects of temperature on higher meiofauna taxa

Nematodes and copepods (and other higher meiofauna taxa) responded differentially to temperature treatments. More specifically, nematode densities decreased in both elevated constant and fluctuating temperature treatments compared to the control in both communities. This result confirms the findings by Mevenkamp et al. (2018) for nematode densities from the same temperate location as used in our study under constant temperature increase, even though the magnitude of temperature change in that study was smaller (+3 °C) than in ours. Our results are also in agreement with Gingold et al. (2013) for two tropical nematode assemblages at constant elevated temperature of a similar range of increase to what was applied here (+5 °C). By contrast, different results were revealed by other experiments testing the combination effects of ocean acidification and global warming. Lee et al. (2017) and Sarmento et al. (2017b) demonstrated that nematode abundances of tropical subtidal communities increased with elevated temperature and lower pH in combination. Again, the temperature of both treatments and controls used in the above experiments were much lower from the range used in our experiment.

Harpacticoid copepods, in contrast, exhibited higher abundances in the elevated constant temperature treatment, but only in the tropical community. Mevenkamp et al. (2018) also found higher copepod densities in the temperate community at their elevated temperature treatment (but note that their elevated temperature was much lower than ours, even lower than our control temperature). Positive short-term effects of elevated temperature on copepod abundances may result from a re-allocation of energy from somatic growth to reproduction (Fitzer et al., 2012; Meadows et al., 2015; Sarmento et al., 2017a). However, nauplii abundances in our experiment remained low in all treatments. Alternatively, the increased copepod abundance in the elevated temperature treatment of the tropical community could also be explained by increased microalgae abundance, as a more prominent biofilm was observed in this treatment towards the end of the experiment (pers. observ.).

Other meiofauna taxa generally exhibited either negative or non-significant but negative effects of elevated temperature treatments on absolute abundances. Specifically, tropical polychaetes and tardigrades and temperate oligochaetes, turbellarians and amphipods were negatively affected by both elevated temperature regimes. Time in some cases had an equally pronounced negative effect on the abundance of some taxa as temperature, but their very low abundances do not allow firm conclusions (see also Meadows et al., 2015). These divergent responses of major taxa at both elevated constant and fluctuating temperature were also apparent when comparing the community composition between temperature treatments (significant temperature, time and interaction effects for both tropical and temperate communities, results not shown here), which is in agreement with Mevenkamp et al. (2018) for the temperate community.

4.3. Effects of temperature on nematode assemblage structure and feeding group composition

Nematode assemblage structure was affected by temperature and time in both tropical and temperate assemblages. However, temperature and time effects were independent in the tropical assemblage, whereas their interactive effect caused changes in the temperate assemblage. For the latter, overdispersion was demonstrated for the

temperature effects alone, nevertheless that was not the case for the temperature and time interaction. Such increased variability is often considered as an indication of lack of stability in a community response (e.g., Tilman, 1996; Emmerson et al., 2001), and in the present experiment may therefore reflect a stress effect of temperature conditions on nematode assemblages.

Species-specific tolerance to elevated temperatures and extremes was observed among nematode species, which may have contributed to the divergent responses of the two communities in terms of species composition. Dominant species tended to remain abundant under elevated temperatures, suggesting they are thermal-stress tolerant. However, species-specific tolerances to certain temperature conditions can be altered by interactions among species and vice-versa, species interactions can be altered by temperature fluctuations. Divergent tolerances of different nematode species to elevated temperature (in combination with low pH) were also revealed within a tropical shallow-water assemblage by Lee et al. (2017), suggesting that changes in fitness of individual species can alter the relative competitiveness of species within the assemblage (Stachowicz et al., 2007). Two recent studies have demonstrated that both elevated constant and fluctuating temperature regimes can substantially affect the interactions between coexisting and competing marine nematode species, revealing divergent responses of population dynamics with respect to increased constant vs fluctuating temperature (De Meester et al., 2015; Vafeiadou et al., 2018). Such shifts in interactions, rather than a differential tolerance *per se*, might also explain the increase and decrease in relative abundance of *Ascolaimus* sp. and *Bathylaimus* sp., respectively, in the temperate assemblage under elevated temperature regimes.

However, 'competitive release' should not be interpreted as a release from competition only, but also as a release from other adverse species interactions such as predation. In our experiment, temperature regime shifted the relative abundances of feeding groups. Overall, predatory/omnivorous (2B) nematodes maintained their high densities throughout the experiment. Their proportional abundances increased considerably more with time in the tropical than in the temperate assemblage, which may explain why in the former, total meiofauna abundances decreased with time (see above, 4.2). In addition, predation pressure can be selective and could have contributed to the observed shifts in assemblage composition, for instance by alleviating competitive interactions among prey species (dos Santos and Moens, 2011).

The fact that predacious nematodes as a group maintained their high abundances throughout the experimental incubations was unexpected, because traits characteristics of this group, such as a large body size, high longevity, low fecundity and slow maturation, are usually associated with a lesser tolerance to environmental disturbance (Alves et al., 2014; Schratzberger et al., 2007). However, the high abundances of predatory nematodes in our experiment could largely be attributed to a few dominant species: *Oncholaimus* sp. was consistently the most abundant species in the tropical assemblages and *Viscosia* sp.2 increased in abundance in the fluctuating temperature treatment, while *E. longispiculosus* and *A. fuscus* remained highly abundant in the temperate assemblages at all temperature treatments. Other, less abundant species (e.g., *Choanolaimus* sp., *Latronema* sp., *Pontonema* sp. in the tropical assemblage; *Odontophora* sp. in the temperate assemblage) were lost due to the enclosure effect or remained rare. Oncholaimidae are typically among the most abundant nematodes of the intertidal zone in sandy beaches (Gheskiere et al., 2004), which may explain the high tolerance of *Oncholaimus* sp., *A. fuscus* and *Viscosia* sp. to fluctuating and elevated temperature regimes. The persistence of 2B nematodes in both tropical and temperate assemblages could further be explained by the removal of macrofauna, which could otherwise have affected 2B nematodes through predation, interference and/or resource competition (Li et al., 1996). Furthermore, a flexible feeding strategy may also render 2B nematodes more successful in microcosm incubations. For instance, Oncholaimidae are facultative predators which not only feed through predation, but also by scavenging and perhaps even microbivory (Moens et al., 1999; Moens and Vincx, 1997). Similarly, *E. longispiculosus* can graze on microalgae in addition to being a predator of meiofauna and ciliates, depending on food availability (Moens et al., 2014).

In our experiment, a dense biofilm was observed from 15 days onwards in the tropical microcosms. This biofilm became denser in the elevated temperature treatments and with time (pers. observ.). At the same time, prokaryotic abundance and biomass increased in the elevated temperature treatment compared to the control after 30 days (data available in Fig. ESM7), resulting in a higher food supply for nematodes at the elevated temperature regime (Gingold et al., 2013). The increase of epistrate feeders (2A) with time in the tropical assemblage is also in line with the observation that microalgal biofilms became more prominent, because 2A nematodes are often microalgal grazers (Moens and Vincx, 1997), although their abundances may also correlate with densities of prokaryotes (Danovaro and Gambi, 2002).

4.4. Effects of temperature on nematode diversity

In contrast with nematode species composition, structural diversity (species richness, Shannon diversity and evenness) of both assemblages was not significantly affected by temperature or time. Hence, biodiversity indices did not reflect the changes in assemblage composition, in accordance with other recent studies on meiofauna and/or nematodes (Meadows et al., 2015; Martinez et al., 2018). However, it is possible that the incubation period was too short to translate observed shifts in species composition to measurable changes in diversity.

Correspondingly, trophic diversity (here ITD^{-1}) also did not show consistent results with species composition in response to temperature regime for the tropical assemblage, which corroborates results by Gingold et al. (2013); in the present experiment, this lack of a significant effect was likely mainly due to overdispersion of the interaction effects. In contrast, results for ITD^{-1} of the temperate assemblage in our experiment did follow the trends of assemblage structure and feeding group composition.

Given the inconsistent response of diversity indices to temperature regime, we strongly recommend not to use biodiversity indices *per se* but only in combination with community/assemblage composition when assessing impacts of environmental stressors, in agreement with Meadows et al. (2015), since the diversity measures appear not to adequately reflect the short-term changes in community composition. While diversity may affect ecosystem functioning (Hooper et al., 2005; Loreau et al., 2001), this also holds for species and functional trait composition (Naeem and Wright, 2003; Petchey and Gaston, 2002). Variations in community composition are generally associated with variations in functional diversity (Petchey and Gaston, 2002). Hence, even small changes in community composition can affect functional trait distribution of a community and may have implications for ecosystem functioning (Schwartz et al., 2000), depending on the traits of the affected species.

4.5. Divergent responses to thermal stress in tropical vs temperate assemblages

Both the tropical and temperate nematode assemblages showed significant changes in response to temperature regime. Total nematode abundances of both assemblages were negatively impacted by the elevated constant and the fluctuating temperature regime, but this effect was considerably more pronounced for the tropical than for the temperate assemblage (density reductions of 59% and 18%, respectively). The tropical assemblage nevertheless appeared particularly more sensitive to the fluctuating than to the constant elevated temperature, because its species composition differed significantly between the fluctuating temperature treatment on the one hand, and both the control and elevated constant temperature treatment on the other. At first glance, our results thus concur with the hypothesis that tropical

assemblages are more sensitive to thermal stress due to their narrower thermal 'safety margins' and their more limited tolerance to temperature fluctuations than their temperate counterparts. On the other hand, tropical assemblages were expected to respond differently under elevated constant temperature as they already experience habitat temperatures that approach their upper tolerance limits in nature (Nguyen et al., 2011; Somero, 2010). Tropical species in our experiment were generally able to cope with the elevated constant temperature, which was probably within the range these species can tolerate, while they suffered from the fluctuating temperature regime. Indeed, rear-edge (that is, warm and low-latitude) population responses to thermal stress may be better explained by changes in amplitude of temperature fluctuations and by increased temperature peaks, rather than by increases in mean temperatures (Bennett et al., 2015).

In contrast to the tropical assemblage, the species composition of the temperate assemblage did not differ significantly between the two elevated temperature regimes; however, both (FT and EC) differed significantly from the control assemblage, and assemblage dissimilarities with the control were of similar magnitude. Temperate intertidal species experience substantial daily and seasonal temperature fluctuations in their natural habitat and tend to live at temperatures well below their upper physiological tolerance limits (Kingsolver et al., 2013; Sunday et al., 2014; Vasseur et al., 2014). Nevertheless, significant shifts in species composition occurred in the temperate assemblage at constant elevated temperature and, similar to the tropical assemblage, also at fluctuating temperature. Whether this reflects sensitivity to the (amplitude of the) fluctuations or to daily elevated peak temperatures (Vasseur et al., 2014) remains to be established. However, except for the effect size on total nematode abundances, our data do not seem to support the hypothesis that temperate assemblages are more tolerant to temperature fluctuations than their tropical counterparts.

4.6. Experimental constraints

It is important to consider that our study was limited to a short period of time (30 days), as for many species the duration of the experiment was probably less than a single generation time. While physiological plasticity may improve species survival in the short term, it can be insufficient to do so, or can even reduce the fitness of organisms that are exposed to thermal stress for a longer period of time (Nguyen et al., 2011). Therefore, longer-term experiments are required to investigate the response of meiofauna and/or nematode communities to climate change effects. The microcosm design used here may contribute to the feasibility of such longer-term experiments.

Another restriction that should be considered is the continuous submersion of the high intertidal communities during our experiments. Although sediments were collected from a zone where organisms are submerged for only a couple of hours per day, tidal effects were not taken into account in our study for practical reasons, in order to isolate temperature effects. Trying to simulate tidal effects in a microcosm design would be technically possible, but as temperature was homogeneous in our microcosms (and not depth-stratified), it would have been difficult to address the combined effects of temperature and tidal exposure. However, that change of tidal conditions may also have an effect on the communities' response (see below). On the other hand, intertidal rather than subtidal sediments were chosen in our experiment because intertidal sediments are naturally more exposed to the fluctuating temperature regimes and temperature extremes that are expected to be part of future climate change scenarios, and thus, more suitable for our experimental approach.

Further, vertical migration of nematodes is known to occur in response to temperature variations, especially in sandy sediments (Maria et al., 2016, and references therein). Short-term vertical migrations could provide a temporary refuge from the most extreme consequences of temperature stress (direct temperature effects on meiofauna physiology and activity, indirect effects through sediment desiccation, increased pore water salinity and decreased oxygen concentration) for meiofauna in response to diurnal peak temperatures occurring mainly during low-tide exposure. The ability to migrate vertically undoubtedly differs among species (e.g., Maria et al., 2012; Steyaert et al., 2001, 2003) and is also related to biotic interactions (Maria et al., 2012), which in turn may differentially affect fitness of populations and hence the outcome of species interactions. But even the strength and/or nature of species interactions may change in response to a shift in temperature regime, as demonstrated for horizontal interactions among cryptic species of the nematode *Litoditis marina* (De Meester et al., 2015).

Moreover, vertical migrations may be more pronounced in sandy beaches compared to muddy tidal flats (Maria et al., 2012; Moens et al., 2013), resulting in a different probability of such migrations mediating temperature impacts on meiofauna in the tropical vs the temperate location studied here (with a coarser and finer grain size, respectively). Since the shallow sediment column and overlaying water in our experiment were maintained at a homogenous temperature from top to bottom, meiofauna could not (temporarily) escape from temperature impacts, and hence direct temperature effects on overall abundances may be expected to have been somewhat more pronounced compared to a field situation. However, indirect effects, through desiccation and fluctuations in salinity and oxygen concentration were excluded in our experimental design and would likely add to the direct temperature impacts in a natural setting. Moreover, effects on assemblage composition are perhaps even more difficult to extrapolate to a field situation because of differential sensitivities of species to the indirect temperature effects, and because of the differential abilities of species to migrate vertically.

5. Conclusions

The present work highlights a different response of meiofauna and nematode communities originating from intertidal tropical and temperate areas to increased constant and fluctuating temperature regimes. In agreement with the hypothesis that tropical species are generally more stenothermic, the tropical nematode assemblage was more affected by the fluctuating than by the constant elevated temperature regime, and its tolerance to the elevated constant temperature treatment suggests that the applied temperature was still within the thermal window of a majority of species in this assemblage. In the temperate nematode assemblage, the response to a fluctuating temperature regime with integrated episodes of elevated temperature maxima was very comparable to the response to a constant elevated temperature. The fluctuating temperature regime significantly affected nematode abundance and species composition of both assemblages despite latitudinal differences, contradicting our hypothesis that tropical nematode assemblages would be comparatively less tolerant to thermal-stress induced regimes.

The results of this study also demonstrate that short (a few hours per day) episodes of substantially elevated maximum temperatures, such as during heat waves, affect species composition as well as functional trait distribution in nematode assemblages, which may well have repercussions for benthic ecosystem functioning. The observed shifts in dominance of the most abundant species indicated an assemblage response to change that can only be properly interpreted by assessing species composition; the taxonomic and functional diversity indices used here did not reflect the actual responses of the two nematode assemblages to increased temperature regimes. It is possible that these shifts in abundances alter the interspecific interactions and thus, may alter the dynamics within assemblages and communities and consequently affect their function in the ecosystem.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2018.10.005.

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